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Multiple Sources of Eastern Filbert Blight Resistance Provide Breeding Utility in New Jersey

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Abstract

The disease eastern filbert blight (EFB), caused by Anisogramma anomala, has prevented commercial hazelnut (*Corylus avellana*) production in eastern North America. Recently, several new sources of resistance to EFB have been identified and genetic improvement efforts are underway in multiple regions of the U.S. to develop adapted, disease-resistant cultivars. However, the wide genetic diversity of the pathogen may confound breeding efforts. In this study, we examined six sources of EFB resistance: *C. avellana* 'Ratoli' and OSU 495.072, *C. americana* 'Rush' and 'Winkler', *C. heterophylla* 'Oygoo', and the Turkish tree hazel (*C. colurna*) hybrid 'Grand Traverse'. Genotypes representing each resistance source were crossed with susceptible parents resulting in a total of 2,947 seedlings in 46 full-sib progenies. They were field planted at Rutgers University and exposed to the disease over a minimum of six years. Their disease response was evaluated on a scale of 0 to 5 (0 = resistant, 5 = highly susceptible) and segregation patterns were examined. All sources transmitted resistance to their offspring in a dominant manner. Interestingly, segregation patterns compiled by resistance source were relatively similar, with about 50% of the plants showing resistance (rating = 0). The remaining trees in each group were characterized as susceptible, with a majority rated as 4 or 5. These results suggest control by one or a limited number of genes, agree with previous linkage mapping work for several of the sources, and show that resistance has been effective when exposed to multiple isolates of *A. anomala*. Our results demonstrate transmission of resistance at a high level and suggest that these sources hold considerable promise for breeding plants adapted to New Jersey and other parts of the eastern U.S.

Hazelnut (*Corylus avellana*) ranks sixth in world tree nut production behind cashew (*Anacardium occidentale*), almond (*Prunus dulcis*), walnut (*Juglans regia*), chestnut (*Castanea* sp.), and pistachio (*Pistacia vera*). Approximately 60-70% of the world's hazelnut crop is produced in Turkey (743,455 t in 2016), followed by Italy (≈ 10%), the Republic of Georgia (≈ 5%), and the U.S. (≈ 5%), with Azerbaijan, Chile, China, Iran, and Spain contributing to the remaining production (Food and Agriculture Organization of the United Nations, 2018). Ninety-nine percent of U.S. production comes from the Willamette Valley of Oregon. Hazelnuts are obligately outcrossing, highly heterozygous, and genetically diverse, with commercial production based on clonally propagated cultivars (Gökirmak et al., 2009; Muehlbauer et al., 2014)

The lack of hazelnut production in the eastern U.S. is largely due to the disease eastern filbert blight (EFB) caused by the fungus *Anisogramma anomala*. This pathogen is native to eastern North America where it is harbored by the wild American hazelnut, *C. americana*. While the wild species is tolerant, EFB is devastating to most plants of *C. avellana*, where it causes large stem cankers, branch die-back, and eventual tree death (Capik and Molnar, 2012; Johnson and Pinkerton, 2002). In the absence of this fungus, hazelnut production thrived for nearly 100 years in the Pacific northwestern

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U.S. (PNW) (Thompson et al., 1996). Unfortunately, despite quarantine efforts (Barss, 1930), *A. anomala* was inadvertently introduced into southwestern Washington, probably around 1960, causing severe orchard damage and loss (Davison and Davidson, 1973; Gottwald and Cameron, 1980). Today, EFB has spread throughout the Willamette Valley. Fungicide sprays, scouting, and pruning of infected stems are effective for managing the disease, but they add considerable expense to production. As such, developing and utilizing EFB-resistant cultivars is considered to be the most cost-effective, long-term means for control (Johnson et al., 1996; Julian et al., 2008, 2009; Thompson et al., 1996).

The first EFB-resistant European hazelnut identified was 'Gasaway', a late-blooming pollinizer now considered obsolete (Cameron, 1976). 'Gasaway' resistance is conferred by a dominant allele at a single locus on hazelnut linkage group (LG) 6 (Coyne et al., 1998; Mehlenbacher et al., 1991, 2006; Osterbauer et al., 1997; Sathuvalli et al., 2017). To date, 'Gasaway' has been widely used in the Oregon State University (OSU) hazelnut breeding program, leading to the development of the EFB-resistant cultivars Santiam (Mehlenbacher et al., 2007), Yamhill (Mehlenbacher et al., 2009), Jefferson (Mehlenbacher et al., 2011), Dorris (Mehlenbacher et al., 2013), Wepster (Mehlenbacher et al., 2014), and McDonald (Mehlenbacher et al., 2016), along with a series of associated pollenizers. Largely based on these cultivars, the Oregon industry has expanded ~12,000 ha over the past eight years (S. Mehlenbacher, personal communication).

Despite the widespread use of the 'Gasaway' *R* gene in Oregon, concern about its long-term durability led researchers to seek additional sources of resistance. Hundreds of *C. avellana* cultivars, seedlings, and interspecific hybrids have since been evaluated for EFB response and around 2-3% have displayed resistance or tolerance to the pathogen. Many of these are now being used in breeding and research efforts at OSU (Chen at al., 2005, 2007; Colburn et al., 2015; Coyne et al., 1998; Leadbetter et al., 2016; Lunde et al., 2000; Sathuvalli et al., 2010, 2011a, 2011b; S.A. Mehlenbacher, personal communication). It is important to note that EFB in the PNW is believed to be from a single point introduction (Pinkerton et al., 1998). Recent work using microsatellite markers for *A. anomala* supports this premise and shows the EFB fungus to be very uniform in the PNW but genetically diverse across its native range in the East (Muehlbauer, 2017; Tobia et al., 2017). Thus, immediate concerns exist for the possible introduction of new, more virulent isolates of the fungus into the PNW against which identified sources of resistance may not be effective. Further, the narrow diversity of the fungus present in the PNW also has implications for new cultivars selected as resistant in Oregon if they were to be planted in the eastern U.S. where they would be confronted with a much wider diversity of *A. anomala* isolates. Some cultivars or selections, while useful in Oregon, may prove susceptible to the disease in the east.

To examine this scenario, Molnar et al. (2010a) used greenhouse inoculations to challenge 'Gasaway' and some of its offspring, as well as several other unrelated potential sources of resistance identified in Oregon, with fungal isolates collected from multiple regions across the U.S. Results of the study showed differences between some of the isolates, with those collected from Michigan, Minnesota, and New Jersey capable of infecting plants carrying the 'Gasaway' gene. Longer-term field studies in New Jersey corroborated the greenhouse findings, where multiple trees of 'Gasaway' and its offspring VR20-11, naturally exposed to the fungus in the field, developed EFB (Capik and Molnar, 2012; Molnar et al., 2010b).

Fortunately, a number of selections unrelated to 'Gasaway' were identified at OSU and proved resistant to all isolates of the fungus used in the greenhouse inoculations (Molnar et al., 2010a). These include *C.* avellana 'Ratoli' from Spain (Lunde et al.,

2000) and OSU 495.072 from southern Russia (Sathuvalli et al., 2010), the *C. americana* × *C. avellana* hybrid OSU 541.147 related to *C. americana* 'Rush' (Bhattarai et al., 2017), the *C. colurna* × *C. avellana* hybrid 'Grand Traverse' (Lunde et al., 2000), and the *C. heterophylla* × *C. avellana* hybrid OSU 526.041, a descendant of *C. heterophylla* 'Ogyoo' from South Korea (S.A. Mehlenbacher, personal communication). These genotypes also remained free of EFB in longer-term field evaluations (Capik and Molnar, 2012), and all but OSU 526.041 remain free of disease as of June 2018 following more than 15 years of exposure; note that OSU 526.041 began to show small, inconsequential cankers for the first time in winter 2017 (Molnar, data not shown). These diverse sources of resistance may hold significant value for developing cultivars that thrive in the presence of the fungus without the added expense of fungicide applications. However, further breeding is required as no existing selections derived from these sources has the nut yield and kernel quality demanded by the world hazelnut market.

A sixth source of EFB resistance was derived from Carl Weschcke's work (Weschcke, 1954) in Wisconsin with further development and distribution by P. Rutter (Badgersett Farm) in Minnesota. This population of seedlings is believed to trace in part to *C. americana* 'Winkler' from Iowa (Sathuvalli and Mehlenbacher, 2011) and has shown long-term EFB resistance in the Midwestern U.S. and New Jersey (Capik and Molnar, 2012; Molnar, 2011; Weschcke, 1954). While this population of seed-propagated germplasm has been disseminated widely for decades and demonstrated a high level of EFB-resistance, individual clones and their offspring have not yet been studied.

In total, these six different sources of EFB resistance represent four different species and diverse geographic origins. Based on their proven ability to resist EFB from multiple locations, and in some cases under notably high disease pressure, they may hold considerable promise for breeding plants adapted to eastern U.S. conditions. However, current knowledge of inheritance of resistance to EFB from these sources is either yet to be studied or is based only on anecdotal reports or exposure to only the Oregon isolate of A. anomala. The objective of this study was to investigate these sources of EFB resistance for eastern U.S. conditions, by crossing each with susceptible parents and evaluating the disease response of their seedlings under high disease pressure in the field in New Jersey.

Materials and Methods

Plant materials. Plants representing six distinct sources of resistance ('Ratoli', OSU 495.072, 'Rush', Weschcke/'Winkler', 'Grand Traverse', and 'Oygoo') (Table 1) were crossed with EFB-susceptible parents to examine transmission of resistance to their offspring. A total of 2,947 plants representing 46 full-sib families were evaluated (Tables 2 and 3). In a few cases, the original resistance sources were used as a parent in the cross, but in most cases their selected, EFB-resistant offspring were used. Truncated pedigrees are presented (Tables 2, 3 and 4) and full parentages included in Supplemental Tables 1 and 2 available online at the links provided at the end of the Literature Cited section. Controlled crosses followed methods described in Mehlenbacher (1994) and were made in 2008 through 2011. The results of two progenies from earlier studies are included. Ten of the crosses were made at OSU and 36 were made at Rutgers.

The resulting seeds were collected in mid-to-late Aug. of each year and kept in cold storage until October. They were then stratified in moist peat moss at 4 °C until early March of the following year. Seeds were germinated in the greenhouse (24 °C day/18 °C night with 16-h day length) in wooden planting boxes (61×91×15 cm) containing a peat-based medium. The seedlings were transplanted after 4-6 weeks into #1 (2.8 L) containers using the same media and top-dressed with 5 g of slow-release fertilizer

Table 1. Hazelnut (*Corylus* spp.) accessions with resistance to eastern filbert blight used to study transmission of resistance to eastern filbert blight to their progeny. The linkage group is shown if the resistance gene has been mapped. All source plants are held in the United States Department of Agriculture (USDA) National Clonal Germplasm Repository and have their plant introduction (PI) number displayed.

Source of resistance	Species	Origin	USDA PI #	Linkage Group	Source References
'Ratoli'	*Corylus avellana*	Spain	PI 557167	7	Lunde et al., 2000; Sathuvalli et al., 2011a
OSU 495.072	*C. avellana*	southern Russia	PI 557421	6	Colburn et al., 2015; Sathuvalli et al., 2010
'Rush'/ Yoder#5	*C. americana*	Pennsylvania/Ohio, USA	PI 557022 (Rush)	7	Bhattarai et al., 2017a; Lunde et al., 2000
Arbor Day hybrids (Weschcke/'Winkler')	*C. americana*	Iowa, Wisconsin, USA	PI 557019 (Winkler)	unknown	Chen et al., 2007; Capik and Molnar, 2012; Hammond, 2006
Grand Traverse	*C. colurna*	Michigan, USA	PI 617185	unknown	Farris, 1989; Lunde et al., 2000
'Oygoo'	*C. heterophylla*	South Korea	PI 557323	unknown	Capik and Molnar, 2012

(Osmocote Plus 15N-9P-12K with micronutrients, 5 to 6 months; The Scotts Co., Marysville, OH). Plants were moved outdoors in late May for acclimation under shade cloth (40% shade) until field planting in Sept. or Oct. of the same year. Tree spacing was ~1.0 m in-row by ~3.5 m between rows. Individual progenies were planted in blocks (plants from each progeny planted consecutively in rows) at the Rutgers University Horticultural Farm 1 and Horticultural Farm 3 in New Brunswick, NJ, and the Cream Ridge Fruit Research and Extension Station, Cream Ridge, NJ. Weed control, irrigation, and fertilizer was provided as needed. The seedling trees were not pruned.

Disease exposure, evaluations, and statistical analysis. The trees were exposed to EFB at the research farms through natural spread from many hundreds of nearby infected hazelnut trees with sporulating cankers. Field inoculations were also conducted each year, where stems from local hazelnut plants infected with EFB were gathered, cut into 10-15 cm pieces, and tied into the canopy of seedlings in April (Molnar et al., 2007). Trees were annually rated in the winter months (Dec. – Mar.) using a 0-5 scale developed by Pinkerton et al. (1992), where 0 = no visible EFB, 1 = only a single canker, 2 = multiple cankers on the same branch, 3 = multiple branches with cankers, 4 = over 50% of stems have cankers, and 5 = all stems contain cankers, excluding new basal suckers. The final ratings reported in this study were made in Dec. 2017 through Mar. 2018. Ratings for progenies 00060 and 07022, previously reported by Molnar et al. (2009) and Molnar et al. (2014), respectively, are included for comparison. The final results for each progeny were tabulated and a frequency distribution (histogram) was assembled for each resistance source (Fig. 1) to visualize disease response patterns and infer genetic control of resistance, i.e., multiple gene (quantitative) inheritance verses major gene (qualitative). Chi-squared goodness-of-fit tests were conducted for progeny showing bi-modal results (versus a normal distribution) for segregation ratios of 1 resistant: 1 susceptible or 3 resistant: 1 susceptible. Seedlings rated 0 were considered resistant while those with scores of 1-5 were considered susceptible. These ratios were observed in several previous studies of resistance derived from *C. avellana* (Bhattarai et al., 2017; Chen et al., 2005; Colburn et al., 2015; Leadbetter et al., 2016; Molnar et al., 2009, 2014; Sathuvalli et al., 2011a, 2011b).

Results and Discussion

All 46 progenies representing the six dif-

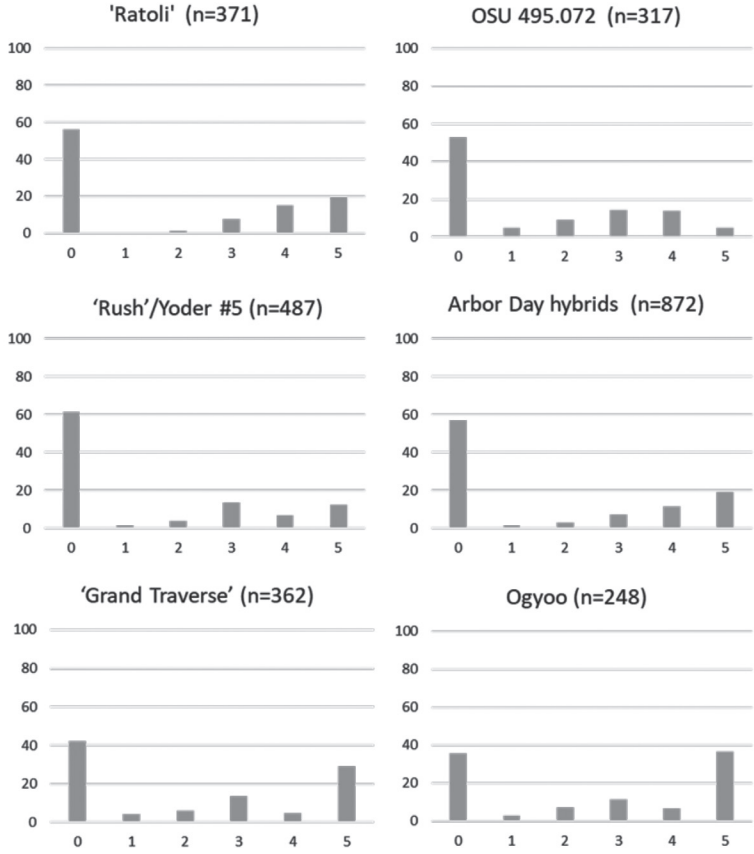

Fig. 1. Histograms of pooled progenies of six sources of resistance to Anisogramma anomala. The proportion (%) of plants in each category is shown, where 0 = no detectable eastern filbert blight; 1 = single canker with fully formed stromata; 2 = multiple cankers on a single branch; 3 = multiple branches with cankers; 4 = greater than 50% of branches contain cankers; and 5 = all branches contain cankers, except basal sprouts. The X-axes represent the categories of disease progression possible for each progeny, while the Y-axes represent the percentage of plants placed in each category.

ferent EFB resistance sources segregated for disease response, with the proportion of resistant seedlings (rating = 0) across the progenies (excluding the three resistant × resistant progeny) ranging from 17.9 – 91.7 % (mean 53%; Tables 2-4). This clear transmission of resistance confirms earlier classification of the six sources as genetically resistant (not escapes from disease) and provides strong support for use in resistance breeding efforts in the eastern U.S. Interestingly, when compiled and analyzed by source of resistance, segregation patterns across each source were relatively similar, where most pooled progenies held at least 50% resistant plants (Fig 1). The histograms show a major peak of plants classified at resistant (rating 0) with the remaining trees in each progeny rated as susceptible, of which a majority were rated as 4 or 5, although the percentages in each cat-

Table 2. Disease response of hazelnut progenies related to *Corylus avellana* 'Ratoli' and OSU 495.072 following exposure to *Anisogramma anomala*, the causal agent of eastern filbert blight (EFB). Disease ratings were on a scale of 0-5 in which 0 = no detectable EFB; 1 = single canker with fully formed stromata; 2 = multiple cankers on a single branch; 3 = multiple branches with cankers; 4 = greater than 50% of branches contain cankers; 5 = all branches contain cankers, except basal sprouts. Based on previous studies in Oregon, examination for fit to a 1 resistant: 1 susceptible model is presented; only seedlings with a score of 0 were considered resistant.

			EFB rating					Observed			
Progeny Code	Female parent	Male parent	0	1	2	3	4	5	Res.	Susc.	χ^2	*P*-value
Corylus avellana 'Ratoli' progeny												
00060	OSU 665.123 (Susc.)	'Ratoli' (Res.)	56	0	0	5	20	25	56	50	0.34	0.56
07022	OSU 1011.001 ('Ratoli' offspring)	OSU 963.017	34	0	0	2	17	11	34	30	0.25	0.62
08555	CRXR06P56 ('Ratoli' offspring)	OSU #4 mix	23	0	0	0	5	13	23	18	0.61	0.43
09502	CRXR04P43 ('Ratoli' offspring)	OSU #6 mix	42	0	1	10	2	15	42	28	2.80	0.09
09503	CRXR06P56 ('Ratoli' offspring)	OSU #6 mix	53	1	4	11	13	8	53	37	2.84	0.09
		pooled	**208**	**1**	**5**	**28**	**57**	**72**	**208**	**163**	**5.46**	**0.02**
C. avellana OSU 495.072 progeny												
09029	OSU 1136.051 (495.072 offspring)	OSU 1031.015	17	1	3	11	16	0	17	31	4.08	0.04
09030	OSU 1136.051 (495.072 offspring)	OSU 1041.069	61	6	17	19	9	2	61	53	0.56	0.45
09031	OSU 1154.027 (495.072 offspring)	OSU 1029.039	23	2	3	1	12	9	23	27	0.32	0.57
08525	OSU 495.072	CRXR13P02 Russian	18	2	3	7	3	1	18	16	0.12	0.73
09567	OSU 495.072	'Tonda Gentile delle Langhe'	38	4	1	2	2	2	38	11	14.88	0.00
09569	OSU 495.072	'Tonda Romana'	11	0	2	5	2	2	11	11	0.00	1.00
		pooled	**168**	**15**	**29**	**45**	**44**	**16**	**168**	**149**	**1.14**	**0.29**

egory varied by source and susceptible parent. This pattern suggests control by a dominant allele at single locus where the resistant parent carries the allele in the heterozygous state, which is congruent with *R*-gene linkage map studies at OSU for several sources as described subsequently. These results are promising with respect to breeding for durable resistance, as they suggest that segregation ratios are similar in Oregon and New Jersey, which is unlike that found with the 'Gasaway' *R*-gene (Muehlbauer et al., 2018). Of further interest, some progenies showed a small peak of individuals classified as 3 for disease response, suggesting that genes for tolerance (quantitative resistance) were also present and segregating in these populations (Osterbauer et al., 1997).

Corylus avellana 'Ratoli'. 'Ratoli' is a minor cultivar from Tarragona, Spain. Lunde et al. (2000) identified it as resistant to EFB through greenhouse inoculations in Oregon. Later, Sathuvalli et al. (2011b) showed that segregation patterns from 'Ratoli' in Oregon were consistent with a dominant allele at a single locus and assigned the resistance locus to LG 7 based on co-segregation with SSR markers. Note that the 'Gasaway' R-gene has been assigned to LG 6 (Mehlenbacher et al., 2006). Five 'Ratoli'-related progenies comprising 371 seedlings were examined in this study. Progeny 00060 was a direct cross between 'Ratoli' (male) and the susceptible selection OSU 665.123 (female). The four other progenies were from crosses of selected EFB-resistant offspring of 'Ratoli' with EFB-susceptible OSU selections. All five progenies individually fit the 1 resistant: 1 susceptible model, confirming reports of control by a dominant allele in heterozygous state at a single locus (Sathuvalli et al., 2011b). However, each of the five progenies showed a slight overabundance of resistant seedlings. Thus, when data for the progenies were combined, the merged data no longer fit the expected model (Table 2; Fig. 1). Segregation distortion is not uncommon in hazelnut and was observed in progenies segregating for resistance from 'Zimmerman' (Lunde et al., 2006), OSU 759.010 from the Republic of Georgia (Sathuvalli et al., 2011b), and 'Culpla', 'Crvenje', and OSU 495.072 (Colburn et al., 2015). Despite the distorted segregations, in these cases each resistance

source still mapped to a single locus. Based on its demonstrated ability to resist EFB from multiple locations and placement on a different LG than 'Gasaway', 'Ratoli' presents a very promising option for breeding eastern U.S. adapted cultivars and potential gene pyramiding.

Corylus avellana OSU 495.072. OSU 495.072 was selected from plants grown from seeds sent to OSU in 1989 from the N.I. Vavilov Research Institute of Plant Industry in St. Petersburg, Russia. It is believed that the seeds originated from a cultivar collection in southern Russia. Sathuvalli et al. (2010) determined it to be resistant to EFB in Oregon through greenhouse inoculations. Later, Colburn et al. (2015) examined segregation patterns of progeny in Oregon when crossed with a susceptible parent and also mapped the location of the *R*-gene using co-segregation with SSR markers. While their results showed that most progenies held an abundance of resistant seedlings that did not fit either a 1:1 or 3:1 segregation ratio, resistance was mapped to a single locus on LG 6 in the same region where the 'Gasaway' *R*-gene is located. The authors suggested that resistance was likely part of a cluster of different resistance genes in the same region.

Six OSU 495.072-related progenies totaling 317 seedlings were examined in this study. Note that three progenies (09029, 09030, and 09031) were from the similar crosses examined in Colburn et al. (2015). When all six progenies were pooled, the OSU 495.072 population fit a 1:1 resistant: susceptible segregation ratio (Table 2; Fig. 1). However, there was some interesting variation among progenies, which is likely from the susceptible parent's contribution. Four of six fit the expected 1: 1 model (09030, 09031, 08525, and 09569), whereas progeny 09567 had an abundance of resistant seedlings with 38 of 49 rated 0 (77.6%). In contrast, progeny 09029 held only 17 of 48 free of EFB (35.4%). This progeny is especially interesting, as Colburn et al. (2015) reported that 41 of 60 trees from this same parental cross evaluated in Oregon were scored resistant to EFB, presenting contrasting results to our data (note that progenies 09030 and 09031 had similar ratios of resistant to susceptible trees visualized in both studies). However, in general our results confirm reports from Oregon that the OSU 495.072 source of resistance is transmitted in a dominant manner and controlled at a single locus. Our somewhat varied responses with the different susceptible parent may indicate interactions with uncharacterized modifying factors present or absent in some parental combinations, of which further work will elucidate. These interactions could also explain the abundance of seedlings rated 3, which indicates a useful level of tolerance, and was not expected based on the choice of known susceptible parents used in the crosses.

Further, in respect to placing the *R*-gene on LG 6, Muehlbauer et al. (2018) examined the EFB response of 1,319 seedlings from 31 different full-sib progenies expected to segregate for the 'Gasaway' *R*-gene in either a 1 resistant: 1 susceptible or 3 resistant: 1 susceptible ratio based on prior work in Oregon. They found that the number of trees remaining free of EFB was much less than the expected ratio. In contrast, nearly all progeny of OSU 495.072 tested in New Jersey segregate as in Oregon, and the parent trees, unlike 'Gasaway', also remain free of EFB. This indicates that the R-gene in OSU 495.072, while located on LG 6, is different than the 'Gasaway' gene, as was suggested by Colburn et al. (2015).

Corylus americana 'Rush'. 'Rush', a wild hazelnut selection from Pennsylvania, has a long history of use in breeding hybrid hazelnuts. It was a parent in the first crosses with *C. avellana* starting in the early 1900s, from which selections were made and clonally propagated, and of which many open-pollinated seedling populations were subsequently grown (Crane et al., 1937; Grimo, 2011; Molnar, 2011; Molnar et al., 2005, 2015; Reed, 1936; Slate, 1961; Thompson et al., 1996). Grower reports in the eastern U.S.

suggest that a number of selections related to 'Rush' have remained free of EFB over many decades of exposure. No signs or symptoms of EFB were found on six of seven accessions related to 'Rush' ('Reed' came down with EFB) in field studies by Capik and Molnar (2012) and greenhouse studies using its offspring OSU 541.147 (Molnar et al., 2010a), as mentioned previously. These results corroborate those of Coyne et al. (1998), who evaluated eight 'Rush' hybrids in Oregon and found no EFB after greenhouse inoculation. In addition, NY 398, NY 616, and Grimo 208P (all offspring of 'Rush') have shown no disease in Niagara-on-the-Lake, Ontario, Canada, for many decades in the presence of susceptible plants with EFB cankers (Grimo, 2011).

The hybrid selection Yoder #5 is an interspecific hybrid seedling selection from R. Yoder of Smithville, OH, that was obtained by S.A. Mehlenbacher in the late 1980s. Lunde et al. (2000) subjected Yoder #5 to greenhouse inoculation with *A. anomala* in Oregon where it remained free of EFB. Yoder #5 is believed to trace back to 'Rush' based on simple sequence repeat (SSR) marker and linkage mapping analysis (Bhattarai et al., 2017; Sathuvalli and Mehlenbacher, 2011). In the dendrogram of Sathuvalli and Mehlenbacher (2012), Yoder #5 was placed in the same branch with 'Rush' and 16 hybrids known to be offspring of 'Rush'. Further, the SSR marker order was consistent in all three maps in the study, placing the resistance locus on LG 7. The same markers flanked the resistance locus for Yoder #5 and 'Rush', supporting the premise that Yoder #5 is a descendant of 'Rush.'

Five progenies related to 'Rush' and five from Yoder #5 were examined in this study, comprising 167 and 320 total seedlings each, respectively (Table 3). Of these, all but one followed the theme of crossing an EFB-resistant breeding selection from either source with a susceptible pollen parent to examine segregation in the offspring. Progeny 11532 differed, however, as an EFB-resistant 'Rush' descendant (H3R17P01) was crossed with 'Jefferson', an offspring of 'Gasaway' resistant to EFB in Oregon (Mehlenbacher et al., 2011), to examine segregation of the two sources of resistance in the progeny. Also following this approach, an additional progeny (11531) was examined which was the result of a cross of 'Rush'-related H3R17P01 with an EFB-resistant Yoder #5 selection CRXR07P58.

In general, transmission of resistance was very high, whereas the progeny from both sources either fit a 1 resistant: 1 susceptible ratio (5 of 11 total) or held an overabundance of resistant plants. The pooled 'Rush' and Yoder #5 progenies had almost identical segregation patterns, so they were grouped together for the final analysis and discussion (the pooled proportion of resistant plants [Rating = 0] for the 'Rush' progenies and Yoder #5 progenies were 59.9 % and 61.9%, respectively). Excluding progenies 11531 and 11532, which were expected to carry *R*-genes from both parents, the range across the 'Rush' and 'Yoder #5 progenies for proportion of resistant plants per progeny was 52.2 to 91.7% (Table 3). Progeny 11531 fit the 3 resistant: 1 susceptible ratio, which is expected when you cross parents heterozygous for a dominant allele at a single locus. This pattern was also observed in Progeny 11502, to be discussed subsequently, when H3R17P01 was used as a pollen parent in a cross with Arbor Day #10 selected from the Weschcke/'Winkler' hybrids.

Interestingly, progeny 11532 (H3R17P01 × 'Jefferson') did not show an abundance of resistant plants and segregated in a 1 resistant: 1 susceptible pattern, which was not expected considering that both parents should be imparting resistance. However, 'Jefferson', despite carrying the 'Gasaway' *R*-gene (Sathuvalli et al., 2017), gets significant amounts of EFB in New Jersey (Capik and Molnar, 2012), which may also be reflected in its ability to transmit resistance to its offspring in the presence of the fungus populations native to New Jersey.

Table 3. Disease response of hazelnut progenies descended from *Corylus americana* 'Rush' and Arbor Day hybrids (C. *americana* × C. *avellana*) descended from Weschcke/'Winkler' germplasm following exposure to *Anisogramma anomala*, the causal agent of eastern filbert blight (EFB). Disease ratings were made on a scale of 0-5 in which 0 = no detectable EFB; 1 = single canker with fully formed stromata; 2 = multiple cankers on a single branch; 3 = multiple branches with cankers; 4 = greater than 50% of branches contain cankers; 5 = all branches contain cankers, except basal sprouts. Based on previous studies in Oregon for 'Rush', examination for fit to a 1 resistant: 1 susceptible model is presented; only seedlings with a score of 0 were considered resistant.

			EFB rating					Observed			
Progeny Code	Female parent	Male parent	0	1	2	3	4	5	Res.	Susc.	χ^2	*P*-value
C. americana 'Rush'/Yoder #5 progeny												
08517	Grimo 208P ('Rush' offspring)	CRXR13P02 Russian	22	0	1	0	0	1	22	2	16.67	0.00
09559	Grimo 208P ('Rush' offspring)	'Tonda di Giffoni'	32	1	1	4	4	16	32	26	0.62	0.43
09578	OSU 541.147 ('Rush' offspring)	'Tonda Gentile delle Langhe'	12	0	3	2	3	3	12	11	0.04	0.83
09583	OSU 541.147 ('Rush' offspring)	'Tonda Romana'	8	0	1	2	1	3	8	7	0.07	0.80
11532	H3R17P01 ('Rush' offspring)	'Jefferson' (Res., 'Gasaway' offspring)	26	1	1	7	3	9	26	21	0.53	0.47
08035	1038.008 (Yoder #5 offspring)	OSU 978.058	13	1	0	0	0	3	13	4	4.76	0.03
08037	1062.055 (Yoder #5 offspring)	OSU 978.058	32	0	1	0	2	12	32	15	6.15	0.01
09036	776.095 (susc.)	OSU 1049.036 (Res., Yoder #5 offspring)	62	1	10	20	10	4	62	45	2.70	0.10
09501	CRXR3P70 (Yoder #5 offspring)	OSU #6 mix	34	3	2	14	6	1	34	26	1.07	0.30
09508	CRXR11P47 (Yoder #5 offspring)	OSU #5 mix	57	0	0	18	5	9	57	32	7.02	0.01
		pooled[z]	**337**	**8**	**21**	**70**	**36**	**62**	**337**	**197**	**24.40**	**0.00**
11531[y]	H3R17P01 ('Rush' offspring)	CRXR7P58 (Res., Yoder #5 offspring)	39	1	1	3	2	1	39	8	11.75	0.21
C. americana × *C. avellana* Arbor Day hybrid progeny												
08538	Arbor Day #1	OSU #2 mix	7	1	0	9	13	9	7	32	16.03	0.00
10514	Arbor Day #1	OSU #8 mix	34	2	0	1	7	25	34	35	0.01	0.90
11506	Arbor Day #1	OSU 1156.107	110	1	14	20	4	3	110	42	30.42	0.00
08537	Arbor Day #3	OSU #2 mix	38	0	0	4	10	17	38	31	0.71	0.40
08541	Arbor Day #3	OSU #3 mix	18	0	0	1	0	3	18	4	8.91	0.00
08543	Arbor Day #3	OSU #1 mix	6	0	1	3	2	4	6	10	1.00	0.32
10516	Arbor Day #3	OSU #7 mix	20	0	0	2	8	2	20	12	2.00	0.16
11503	Arbor Day #3	'Jefferson' (Res., 'Gasaway' offspring)	63	5	12	13	7	20	63	57	0.30	0.58
11506	Arbor Day #3	OSU 1156.107	25	0	1	3	7	10	25	21	0.35	0.56
08539	Arbor Day #10	OSU #3 mix	17	2	0	0	1	2	17	5	6.55	0.01
09608	Arbor Day #10	OSU #5 mix	84	1	0	5	25	29	84	60	4.00	0.05
09609	Arbor Day #10	OSU #6 mix	42	0	0	1	9	27	42	37	0.32	0.57
10517	Arbor Day #10	OSU #7 mix	35	0	0	2	7	18	35	27	1.03	0.31
		pooled[z]	**687**	**26**	**34**	**82**	**110**	**176**	**687**	**428**	**18.21**	**0.00**
11501[y]	Arbor Day #10	CRXR11P07 (Res., 'Grand Trav'. offspring)	99	4	2	9	4	5	99	24	1.98	0.16
11502[y]	Arbor Day #10	H3R17P01 (Res., 'Rush' offspring)	89	10	4	9	6	2	89	31	0.04	0.83

[z] 3:1 progeny excluded from pooled chi squared test.
[y] Chi squared test examines expected ratio 3 resistant: 1 susceptible ratio based on crosses of two EFB-resistant parents.

On a further point of discussion, progeny 08517, a cross of Grimo 208P (Carmela™; NY 1329 [*C. americana* 'Rush' × *C. avellana* 'Cosford'] × OP) × CRXR13P02 (EFB-susceptible *C. avellana* from southern Russia), yielded an unusually high percentage of resistant plants. Of the 24 plants examined, 22 showed no EFB, one was rated 2 (minor infection), and the final tree was rated 5. However, Progeny 09559 (Grimo 208P × 'Tonda di Giffoni') differed considerably with 32 trees classified as resistant and 26 susceptible (fitting the expected 1 resistant: 1 susceptible model) (Table 4). Interestingly, when EFB-susceptible CRXR13P02 was crossed with OSU 495.072 (Progeny 08525), there seemed to be no added contribution towards EFB resistance as that progeny also segregated in the expected 1 resistant: 1 susceptible pattern (Table 2). These data may suggest an epistatic gene interaction between Grimo 208P and CRXR13P02, which merits further investigation.

Collectively, the segregation patterns in

Table 4. Disease response of hazelnut progenies descended from 'Grand Traverse' [(*Corylus colurna* × *C. avellana*) x *C. avellana*] and *C. heterophylla* 'Ogyoo' following exposure to *Anisogramma anomala*, the causal agent of eastern filbert blight (EFB). Disease ratings were made on a scale of 0-5 in which 0 = no detectable EFB; 1 = single canker with fully formed stromata; 2 = multiple cankers on a single branch; 3 = multiple branches with cankers; 4 = greater than 50% of branches contain cankers; 5 = all branches contain cankers, except basal sprouts. Examination for fit to a 1 resistant: 1 susceptible model is presented; only seedlings with a score of 0 were considered resistant.

			EFB rating					Observed			
Progeny Code	Female parent	Male parent	0	1	2	3	4	5	Res.	Susc.	χ^2	*P*-value
C. colurna × *C. avellana* 'Grand Traverse' progeny												
09504	CRXR09P32 ('Grand Trav.' offspring)	OSU #6 mix	51	7	5	13	5	29	51	59	0.58	0.45
09506	CRXR11P07 ('Grand Trav.' offspring)	OSU #5 mix	45	3	3	14	2	38	45	60	2.14	0.14
09507	CRXR11P10 ('Grand Trav.' offspring)	OSU #6 mix	23	5	9	15	4	11	23	44	6.58	0.01
09553	'Grand Traverse'	'Tonda Romana'	33	1	5	7	6	28	33	47	2.45	0.12
		pooled	**152**	**16**	**22**	**49**	**17**	**106**	**152**	**210**	**9.29**	**0.00**
C. heterophylla 'Ogyoo' progeny												
08547	OSU 526.041 ('Ogyoo' offspring)	'Aurea'	25	2	2	2	2	10	25	18	1.14	0.29
09570	OSU 526.041 ('Ogyoo' offspring)	'Tonda di Giffoni'	7	1	2	2	2	12	7	19	5.54	0.02
09573	OSU 526.041 ('Ogyoo' offspring)	'Tonda Romana'	8	3	3	0	1	21	8	28	11.1	0.00
10021	1181.002 ('Ogyoo' offspring)	OSU 1093.107	17	0	4	8	4	25	17	41	9.93	0.00
10022	1181.002 ('Ogyoo' offspring)	OSU 1178.056	31	1	7	16	8	22	31	54	6.22	0.01
		pooled	**88**	**7**	**18**	**28**	**17**	**90**	**88**	**160**	**20.9**	**0.00**

the 'Rush' and Yoder #5 progenies confirm the findings of Bhattarai et al. (2017) in respect to resistance controlled by a dominant allele at a single locus. Our results are also similar to Bhattarai et al. (2017) in that the frequency of resistant offspring in some progenies exceeded the expected 50%. Further, based on the very similar segregation patterns observed for both sources, our results support the claim that Yoder #5 is a descendant of 'Rush' (Sathuvalli and Mehlenbacher, 2011). Most importantly, the results show that the *R*-gene behaves similarly in New Jersey to Oregon and further confirms past experiences with the plant material, providing strong support for its use in continued breeding. It should also be noted that the plants examined in this study represent multiple generation backcross hybrids to *C. avellana*. Thus, while the *R*-gene is derived from *C. americana*, a species distinguished by its tiny nuts borne in large clasping husks, the phenotype of the plants in this study is largely indistinguishable from *C. avellana*.

Weschcke (*C. americana* 'Winkler') hybrids. 'Winkler' was used extensively by Weschcke in his hybrid breeding efforts in Wisconsin (Molnar, 2011; Weschcke, 1954). Later, Rutter (1987, 1991) relied heavily on Weschcke's material as part of his breeding efforts and plantings in Minnesota from which many EFB-resistant, seed-propagated plants were distributed to farmers and nurseries, including ~5,000 planted at the Arbor Day Farm, Nebraska City, NE. The Arbor Day Foundation has subsequently distributed hundreds of thousands of seedlings from their planting to their members (Molnar and Capik, 2012). From the Arbor Day planting, a number of high-yielding selections were identified (Hammond, 2006). Eleven were clonally propagated and screened at Rutgers for EFB response and six showed no EFB after greenhouse inoculations and multiple years of exposure in the field (Capik and Molnar, 2012; Molnar, data not shown). It is important to note that Sathuvalli and Mehlenbacher (2011) used SSR markers to show that most of the Arbor Day accessions clustered closely with 'Winkler', supporting their reported origins from the Weschcke breeding material. Further, grafted trees of 'Winkler' showed no EFB after more than 6 years of exposure to high EFB pressure in New Jersey (Capik and Molnar, 2012) and Pinkerton et al. (1993) reported that 'Win-

kler' displayed no symptoms or signs of EFB following greenhouse inoculations with *A. anomala* in Oregon. Also, five additional selections related to the Weschcke germplasm source were determined to be resistant (Chen et al., 2007).

In this study, three Arbor Day Farm EFB-resistant selections, Arbor Day #1 (10-50), Arbor Day #3 (11-51), and Arbor Day #10 (11-55), were used in crosses that resulted in three, six, and six different full-sib progenies, respectively, for a total of 1,115 plants. Most followed the approach of crossing an EFB-resistant breeding selection with a susceptible pollen parent to examine segregation in the offspring. However, three progenies were the result of crossing parents each protected by a different resistance source to investigate segregation of two sources of resistance: Arbor Day #3 was crossed with 'Jefferson' and Arbor Day #10 was crossed with the 'Rush' descendant H3R17P01 and 'Grand Traverse' descendant CRXR11P07.

Excluding the three "two-source" progenies, the pooled segregation patterns from all three Arbor Day plants were nearly identical, with resistant plants comprising 58.1%, 55.7%, and 58.0% of the total populations for Arbor Day #1, #3, and #10, respectively. Nearly all progenies showed a slight abundance of resistant plants over the 1 resistant: 1 susceptible ratio, although 9 of fifteen fit the model individually based on the chi squared test (Table 3). Overall, these data suggest control by a dominant allele in the heterozygous state at a single locus. Following in line with these results and that for the 'Rush' source of resistance, progeny 11502 (Arbor Day #10 × H3R17P01) yielded offspring that closely fit a 3 resistant: 1 susceptible ratio, fitting the model for the segregation of two dominant resistance alleles (one contributed by each heterozygous parent). A similar result was found for progeny 11501, where Arbor Day #3 was crossed with CRXR11P07 ('Grand Traverse' resistance source to be discussed subsequently). In contrast, progeny 11503 (Arbor Day #3 × 'Jefferson') segregated in a 1 resistant: 1 susceptible manner similar to progeny 11532 (H3R17P01 × 'Jefferson'), providing further evidence that 'Jefferson' is not likely contributing resistance in this study, while further supporting control at a single locus transmitted from the Arbor Day selections.

'Grand Traverse'. 'Grand Traverse' is reported as (*C. colurna* × *C. avellana*) 'Faroka' × *C. avellana* 'Royal' by its inventor C. Farris, who selected it in Michigan and designated it as EFB resistant (Farris, 1989, 2000). Its incompatibility alleles support it being a seedling of 'Faroka' but do not support 'Royal' as the other parent (Lunde et al., 2000). 'Grand Traverse' was confirmed as resistant to EFB in Oregon (Lunde et al., 2000) and in studies at Rutgers University as mentioned previously (Capik and Molnar, 2012; Molnar et al., 2010a). It also remained free of EFB in long-term field trials at the University of Nebraska, Lincoln (T. Pabst, personal communication). Previously, 'Grand Traverse' was shown to transmit EFB resistance to 25% of its progeny in a field trial in New Jersey, although based on only one progeny (Molnar et al., 2009). Further, 'Lisa', an offspring of 'Grand Traverse', was found to be resistant to EFB in Oregon and New Jersey (Capik and Molnar, 2012; Chen et al., 2007).

In this study, four progenies related to 'Grand Traverse' were examined. One was the result of 'Grand Traverse' directly crossed with EFB-susceptible 'Tonda Romana' (from Italy). The remaining progeny were derived from EFB-resistant selections descended from 'Grand Traverse' (and expected to carry its source of resistance) crossed with susceptible pollen parents. These four progenies yielded a total of 362 plants. Three of four progenies met the chi squared test for fit to a 1 resistant: 1 susceptible ratio, with the fourth holding an abundance of resistant plants. However, the pooled data did not fit the model with only 42.0% of the population remaining free of cankers. Regardless, the bimodal segregation pattern supports control at a single locus. Efforts to map the

'Grand Traverse' *R*-gene, which is thought to be derived from *C. colurna* and thus potentially unique, are in progress. Similar to the plant phenotypes discussed for the *C. americana* 'Rush' progenies, the 'Grand Traverse' progenies also represent multiple generation backcrosses from *C. colurna* to *C. avellana* and at this point are generally indistinguishable from *C. avellana*.

Corylus heterophylla 'Oygoo'. 'Oygoo' (PI 557323) from South Korea was crossed by S. Mehlenbacher at OSU in 1989 with a mixture of three *C. avellana* pollens (OSU 55.129, Birk 5-6, and OSU 226.122) to develop OSU 526.041, of which the male parent has yet to be determined (S.A. Mehlenbacher, personal communication). Selection OSU 526.041 was found to be resistant to EFB in Oregon and then tested by Molnar et al. (2010a) and Capik and Molnar (2012) in New Jersey, where it also remained free of EFB as previously mentioned. The parent tree 'Ogyoo' also expressed no EFB in the field trial, as well as OSU 526.030, a sibling of OSU 526.041 derived from a cross with EFB-susceptible *C. avellana* OSU 226.122. It should be noted that 'Ogyoo' and OSU 526.030 remain free of EFB at Rutgers as of June 2018, but OSU 526.041 has EFB equating to a rating of 2 (high level of tolerance; Molnar unpublished).

Five progenies and a total of 248 seedlings represented resistance from *C. heterophylla* 'Ogyoo' in this study. Three progenies were derived from crosses of OSU 526.041 and susceptible *C. avellana* pollen parents. The remaining two originated from crosses with EFB-resistant OSU 1181.002, which resulted from two generations of backcrossing to EFB-susceptible *C. avellana*. Of the five progenies, only one (08547) segregated in a clear 1 resistant: 1 susceptible pattern. The other four held smaller proportions of resistant trees (35.5% resistant in the pooled data). However, the histograms show a bimodal distribution with major peaks for ratings of 0 and 5 (Fig. 1). Interestingly, these results are similar to what was observed for 'Gasaway' progeny (Muehlbauer et al., 2018) and suggest that a major resistance gene alone can provide a high level of tolerance, but the final plant phenotype depends on interaction with modifying factors contributed by either/both parents. Linkage mapping work in progress will shed light on this source of resistance. These results also confirm responses of 'Oygoo', OSU 526.041, and OSU 526.030 in the field, where 'Ogyoo' and OSU 526.030 remain free of EFB but OSU 526.041 has developed some small cankers.

Conclusions

Overall, this study presents the EFB response of 2,947 seedlings in 46 full-sib progenies representing six different sources of EFB resistance. From these results, and previous work in Oregon and New Jersey, it is apparent that most or all of the *R*-genes investigated are simply inherited and provide resistance or a high level of tolerance under New Jersey conditions, where the pathogen is represented by a wide diversity of *A. anomala* genotypes (Muehlbauer, 2019; Tobia et al., 2019). The resistance sources examined were selected based on their performance against different isolates of *A. anomala* originating in multiple regions across the native range of the pathogen and over longer-term exposure to high disease pressure. The high level of transmission of resistance to their offspring (generally exceeding 50%) and the potential for durable resistance supports their continued used in breeding to combine EFB resistance with high nut yield, good kernel quality, and other desirable traits. Marker-assisted breeding is in use at OSU for the 'Gasaway' source of resistance placed on LG 6 (Davis and Mehlenbacher, 1997; Mehlenbacher et al., 2004). As breeder-friendly markers are developed for these additional six sources, *R*-gene pyramiding will be pursued. Work to explore this approach is currently underway at Rutgers and OSU.

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Supplemental Table 1. Parentage and breeding histories of controlled crosses examined for response to eastern filbert blight.
https://www.researchgate.net/publication/329539791_Supplemental_Table_1_-_full_pedigrees_Molnar_et_al_Transmission_of_six_sources_of_eastern_filbert_blight_resistance_in_New_Jersey

Supplemental Table 2. Pedigrees of Oregon State University (OSU) hazelnut pollen parents used in controlled crosses.
https://www.researchgate.net/publication/329539876_Supplemental_Table_2_-_Pollen_Mixes_Molnar_et_al_Transmission_of_six_sources_of_eastern_filbert_blight_resistance_in_New_Jersey